

A new species of *Raricirrus* (Polychaeta: Ctenodrilidae) from wood collected in the Tongue of the Ocean, Virgin Islands

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Abstract.—*Raricirrus variabilis* new species (Polychaeta: Ctenodrilidae) is described from the Tongue of the Ocean, St. Croix, Virgin Islands. This deep-sea species was collected from submerged wood at 4000 m and is an apparent organic-enrichment opportunist. Taxonomic differences between the genera *Raricirrus* and *Raphidrilus* are discussed. The life history characteristics of this species are examined.

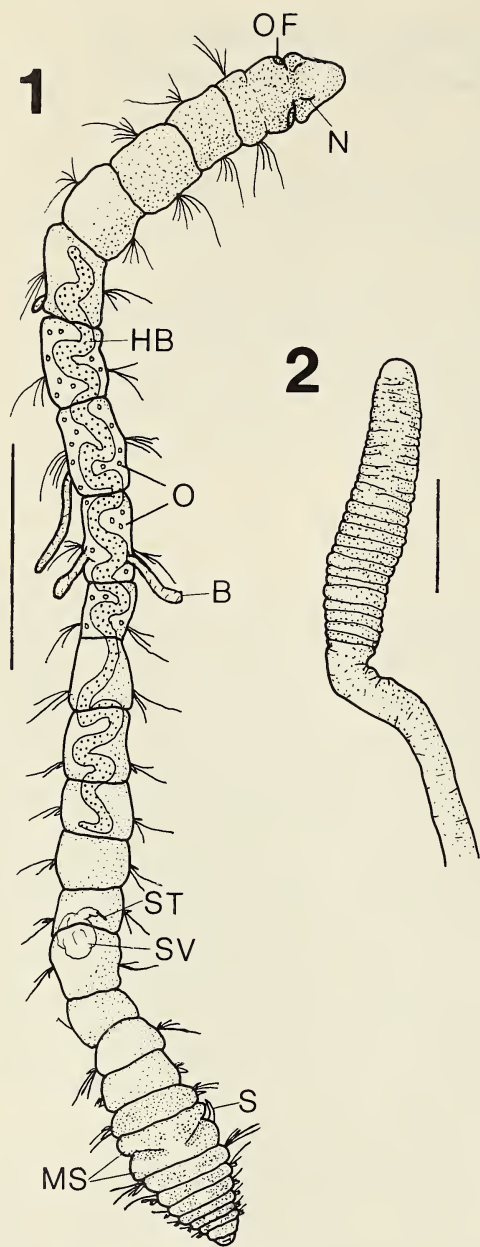
Woody plant material is rapidly broken down in the deep sea by bivalves belonging to the family Pholadidae (Mollusca), subfamily Xylophaginae. The activities of these pholads have been shown to provide a highly concentrated, tractable source of organic material that supports a community of associated organisms (Turner 1973, 1977, 1981). Many of these associated species survive in the deep sea by specifically finding and exploiting organically enriched sites (Grassle & Morse-Porteous 1987, Smith & Hessler 1987, Desbruyères & Laubier 1988). As part of a long-term study of such wood-associated communities by Dr. Ruth Turner, specimens of an undescribed polychaete belonging to the family Ctenodrilidae were recovered from pholad-riddled wood panels and stray wood ("wild wood") retrieved from the deep-sea floor in the Tongue of the Ocean. This paper describes *Raricirrus variabilis*, new species, and further elucidates the separation of two ctenodrilid genera *Raricirrus* and *Raphidrilus*.

Raricirrus variabilis, new species

Material examined.—St. Croix, Virgin Islands: 17°56.63'N, 64°48.6'W, 4000 m. Holotype (MCZ 4008) from wood panel P-13; submerged 17 Dec 1978 (*Alvin* Dive

873), recovered 6 Dec 1980 (*Alvin* Dive 1079). Paratypes (MCZ 4009) 12 specimens from same panel and dates. Paratype (MCZ 4011) one specimen from wood panel P-2; submerged 17 Dec 1978 (*Alvin* Dive 873), recovered 13 Dec 1980 (*Alvin* Dive 1082). Paratypes (MCZ 4010) 6 specimens from wood panel P-12; submerged 17 Dec 1978 (*Alvin* Dive 873), recovered 13 Dec 1980 (*Alvin* Dive 1082). Paratypes (USNM 170552) 8 specimens from wood panel P-5 & P-13 wash material; submerged 17 Dec 1978 (*Alvin* Dive 873), recovered 6 Dec 1980 (*Alvin* Dive 1079). Paratypes (USNM 170553) 4 epitokous specimens from 6 Ft. plank, wild wood; recovered 20 Dec 1978 (*Alvin* Dive 876).

Description.—Benthic form: Body elongate with widened posterior region; anterior and middle body segments longer than wide, posterior segments much wider than long (Fig. 1). Holotype 6.75 mm long, 0.43 mm maximum width (modified segments) with 27 setigers (Table 1, specimen S); paratypes 1.54–7.59 mm long, 0.25–0.61 mm wide, with 18–31 setigers (Table 1). Prostomium conical, eyespots lacking; nuchal organs dorsolateral, appearing as slits or round depressions with what appear to be cilia within. Prostomium with lateral oral folds; pro-



Figs. 1-2. *Raricirrus variabilis*, new species. 1. Dorsal view of holotype (specimen S). B = branchiae, HB = heart body, MS = modified segments, N = nuchal organ, O = oocytes, OF = oral fold, S = enlarged spine, ST = reproductive stylet, SV = seminal vesicle. Scale bar = 1.0 mm. 2. Distal end of branchia (specimen MCZ 4011). Scale bar = 100 μ m.

stomium, peristomium and first setiger continuous dorsally, differentiated ventrally. Body of larger specimens brownish gray, prostomium brown posterodorsally, first two setigers and posterior body region gold brown across dorsum; smaller specimens uniformly pale tan to cream color.

Branchial filaments greatly elongate (approximately 60% of total body length) with club-like ends (Fig. 2), emerging posterodorsal to notopodia. Branchial filaments fragile and easily lost or broken (incomplete branchiae on setigers 5, 7 and 8 in holotype), branchial scars on other segments not discernible; anteriormost occurrence observed at setiger 2, posteriormost on last setiger anterior to the modified segments of an epitokous individual. Heart body a reddish brown convoluted tube (Fig. 1) extending for a variable (range shown in parentheses) number of segments (4-11) beginning on setiger 4 (4-6).

Notosetae and neurosetae emerging directly from body wall, lateral in anterior region, becoming ventrolateral elsewhere. Notosetae of three kinds: four to six capillaries finely serrate distally, usually one (1-3) much longer (ca. $\frac{2}{3}$ body width) than others; short pectinate setae with narrow, widely spaced teeth (Fig. 3A) beginning in anterior half of body, grading into coarsely pectinate falcigers in the midbody region (Fig. 3B), and coarsely serrate setae (Fig. 3C) posterior to the modified setigers. Neurosetae three to six pectinate falcigers (Fig. 3D) increasing in length posteriorly; 1-2 straight, coarsely serrate setae (similar to those of posterior notopodia) in the setigers posterior to the modified setigers (Fig. 4).

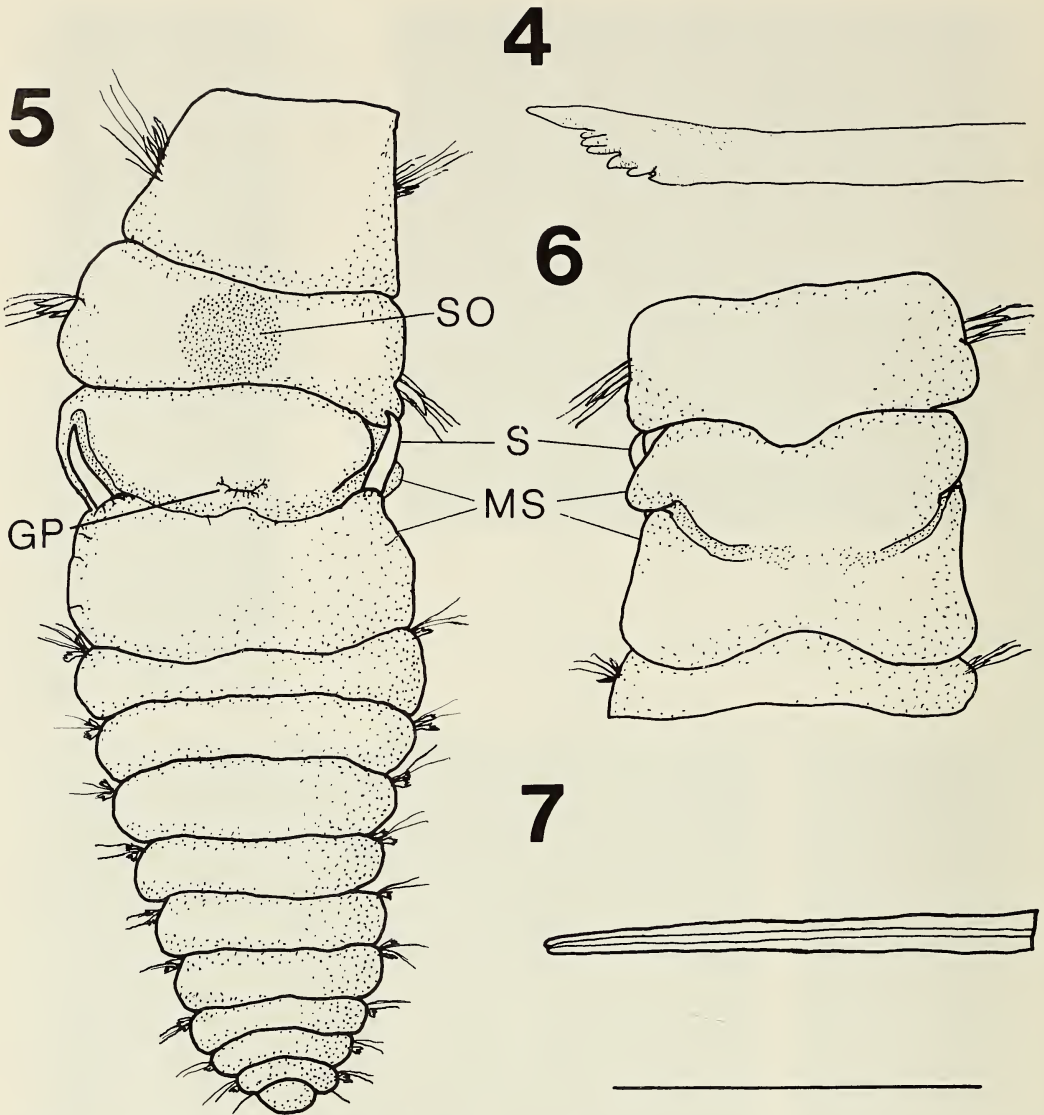
A pair of modified segments present as first two segments of broadened posterior region in all but several smaller (<2.73 mm long) individuals (Table 1). Modified segments distinct dorsally (Fig. 6), with one pair of large, curved notopodial spines emerging anterolaterally from second modified segment (holotype with only a single spine on right side), fitting into deep grooves on posterior ventral surface of first modified



A B _____
 C D _____



Fig. 3. Setae of *Raricirrus variabilis*, new species. A-C. Notosetae: A. Short pectinate falciger with the bases of several capillary setae from anterior region. B. Coarsely pectinate falciger from midbody region. C. Coarsely serrate falciger from region posterior to the modified segments. D. Pectinate neuropodial falcigers from midbody region. Scale bars = 10 μ m.



Figs. 4–7. *Raricirrus variabilis*, new species. 4. Coarsely serrate neuropodial falciger from region posterior to the modified segments. Scale bar = 50 μm . 5. Posterior region of epitokous individual (specimen W), ventral view. GP = genital pore, SO = spherical organ. Scale bar = 500 μm . 6. Modified segments of epitokous individual (specimen W), dorsal view. Scale bar = 500 μm . 7. Reproductive stylet (specimen R). Scale bar = 50 μm .

segment (Fig. 5). Three specimens (including holotype) with a pair of enlarged, straight spines in notopodia of 1–2 setigers anterior to modified segments. Median pore observed on ventral surface of second modified segment (Fig. 5, GP), associated with a medial spherical area within first modified segment or segment immediately anterior

(Fig. 5, SO). Spherical structure appeared empty or sometimes contained diffuse, coarse-grained material when examined in squash preparation. Pygidium rounded with dorsoterminal anus.

Oocytes observed scattered in several anterior setigers of several benthic specimens (numerous 10–25 μm diameter oocytes in

setigers 5–9 of holotype); these setigers often thin-walled and delicate. Straight cuticular stylet (Fig. 7) with narrow lumen present from five to nine setigers (five in holotype) anterior to modified segments in several specimens, associated with a large sac (seminal vesicle) of what were revealed to be spermatozoa in squash preparation (Fig. 1). Presence and development of modified segments apparently unrelated to presence of either observable oocytes or a stylet and seminal vesicle.

Epitokes. — Specimens 6.67–20.64 mm long, 0.73–2.07 mm wide, 28–35 setigers (Table 1). Midbody region brown-gray, clearly differentiated from light cream colored and much narrower posterior setigers. Capillary setae more numerous in notopodial bundles (5–16) and with a greater number (2–9) of elongate capillaries (ca. $\frac{3}{4}$ body width) than in benthic specimens. Notopodial falcigers lacking; straight, coarsely serrate setae present posterior to the modified segments. Neurosetae similar to those of benthic individuals but with a greater number of falcigers (maximum of 8–10). Heart body extending through five to eight setigers starting at setigers 8–10. The body cavity of two epitokous specimens (Table 1, specimens U and X) contained numerous oocytes from setigers 6–8 to the first segment anterior to the modified segments. Maximum diameter of these oocytes was approximately 140 μm and each oocyte contained a round germinal vesicle in the nucleus, and was filled with coarse, yolky material.

Other material. — While trends in morphological characters are apparent, Table 1 illustrates the great morphological variability expressed by this species. The anteriormost occurrence of the heart body (character 4) in benthic forms was in setiger 4, usually extending through 9 segments to setiger 12 (from 4–6 to 7–14); in epitokes from 8–10 to 13–16. Modified segments (character 5) were absent in some smaller specimens and present in the region of setigers

18–22 in larger individuals. The number of setigers posterior to the modified segments (character 6) was variable (2–9 in benthic forms, 9–11 in epitokes), but generally ranged from five to seven in larger benthic individuals.

The variability in the distribution of setal types displayed in the benthic form of *Raricirrus variabilis* made the characterization of body regions based on setal characteristics impossible. The greatest number of capillary notosetae (character 7) occurred in the first or second setiger with from four to seven capillaries per setal bundle, from one to three of these capillaries much longer than the rest. Subsequent notopodia possessed from one to five capillaries with a single elongate capillary per setal bundle. The anteriormost occurrence of notopodial pectinate falcigers (character 11) was usually at setigers 3–9, although the first occurrence of such setae was at setigers 10–13 in several specimens. Coarsely serrate notosetae (character 12) were usually present beginning immediately posterior to the modified segments and were absent in most of the smaller individuals (< 3.20 mm long) analyzed. Several specimens possessed serrate notosetae in the last setiger anterior to the modified segments.

Similar coarsely serrate neurosetae (character 15) were present in all but three of the smaller individuals and were commonly found only in the posterior setigers. Several specimens had coarsely serrate neurosetae in from one to five setigers anterior to the modified segments. Enlarged, curved spines of the modified segments (character 16) usually occurred either as a single or double pair. Several of the specimens with well developed modified segments either lacked enlarged spines or possessed only a single spine.

Three of the four epitokous individuals examined were much larger than any of the other specimens and possessed a greater number of setigers than any of the benthic individuals examined (Table 1). The heart

Table 1.—Summarizes the morphological characters for 20 specimens of the benthic form and four specimens of the epitokous form of *Raricirrus variabilis*, new species. X = character not present. Holotype = specimen S.

Indi- vidual	Character															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
	Benthic specimens															
A	20	1.54	0.25	4-7	X	X	4	1	2	1	3	20	3	2	18	X
B	20	1.95	0.27	4-8	X	X	3	1	2	1	1	X	4	2	X	X
C	24	2.18	0.30	4-11	X	X	4	1	2	1	5	X	4	3-4	24	X
D	25	2.23	0.27	4-12	22-23	2	4	2	1	1	3	X	5	3-4	17	1 + 1
E	20	2.30	0.23	4-10	X	X	3	2	1	1	4	X	4	3-4	X	X
F	18	2.50	0.32	4-7	X	X	6	1-2	1	1	3	X	4	3-4	X	X
G	24	2.57	0.32	4-12	20-21	3	4	1-3	2	1	5	24	5	4-5	22	2 + 2
H	23	2.73	0.25	4-14	X	X	4	1-2	1	1	7	X	4	3-4	14	X
I	27	3.20	0.41	4-12	21-22	5	5	3	2	1	8	23	6	4	23	2 + 2
J	27	3.30	0.43	4-12	18-19	7	5	4-5	3	1	13	21	5	4-5	22	X
K	25	3.41	0.30	4-12	21-22	3	6	3-4	2	1	7	23	6	3-4	23	1 + 1
L	25	3.50	0.36	4-11	21-22	3	5	2-3	1	1	6	23	5	4	23	1 + 1
M	27	3.61	0.30	5-12	21-22	5	4	2-3	2	1	9	23	5	4	23	1 + 1
N	31	3.70	0.40	5-11	21-22	9	5	3-4	1	1	6	20	6	4-5	23	1 + 1
O	29	4.43	0.41	4-12	21-22	7	7	4-5	3	1	3	23	5	4-5	20	1 + 1
P	28	4.57	0.48	6-12	20-21	7	7	3-5	2	1	6	22	6	3-6	22	2 + 2
Q	26	4.57	0.34	4-12	20-21	5	6	3	2	1	7	22	6	3-5	22	0 + 0
R	28	5.41	0.52	4-12	20-21	7	6	4-5	3	1	9	23	6	5-6	22	2 + 2
S	27	6.75	0.43	5-12	19-20	6	6	2-3	2	1	11	21	6	4-5	21	0 + 1
T	28	7.59	0.61	4-12	20-21	7	7	2-3	2	1	10	23	6	3-6	19	2 + 2
	Epitokous specimens															
W	28	6.67	0.73	8-13	18-19	9	8	6-8	4	2-4	X	22	8	5-8	22	1 + 1
V	34	14.16	1.16	9-16	23-24	10	16	11-16	8	4-8	X	25	10	8-10	25	1 + 1
U	35	17.11	2.07	9-15	23-24	12	16	12-15	9	5-8	X	25	11	9-11	25	1 + 1
X	32	20.64	1.27	10-14	20-21	11	12	5-11	6	3-5	X	22	10	5-9	19	1 + 1

1 = number of setigers, 2 = length (mm), 3 = width (mm), 4 = heart body location (range of setigers), 5 = location of modified segments, 6 = number of setigers posterior to modified segments, 7 = maximum number of capillaries in notopodia, 8 = number of capillaries in midbody segments, 9 = maximum number of long capillaries, 10 = number of long capillaries in midbody, 11 = first occurrence of pectinate falciigers in notopodia, 12 = first occurrence of coarsely serrate falciigers in notopodia, 13 = maximum number of neuropodial falciigers, 14 = number of neuropodial falciigers in midbody region, 15 = first occurrence of coarsely serrate falciigers in neuropodia, 16 = reproductive spines.

body of the epitokous specimens did not occur until setiger 8–10, extending to setiger 13–16. Modified setigers were present at the same or slightly more posterior setigers than in the benthic form, but the number of setigers posterior to these segments was greater in the epitokous specimens (9–12).

Epitokous individuals possessed a greater number of capillary notosetae along with a greater number of elongate capillaries in the anterior and midbody setigers. Notopodial pectinate falcigers were absent in the epitokous specimens while serrate notosetae were present only in the segments posterior to the modified segments. Coarsely serrate neurosetae were found only posterior to the modified segments with the exception of one epitokous individual with such neurosetae present in the segment immediately anterior to the modified segments.

Remarks. — *Raricirrus variabilis* differs from *R. maculatus* Hartman, 1961, and *R. beryli* Petersen & George, 1991, in the possession of a more anteriorly situated heart body, the presence of pectinate notopodial falcigers in the benthic stage, the presence of a seminal vesicle and reproductive stylet, and the apparent absence of an asexual reproductive mode. *Raricirrus variabilis* and *R. maculatus* share the presence of a modified region with large curved spines in at least some specimens, although that of *R. maculatus* is a apparently single modified segment while that of *R. variabilis* is composed of two segments incompletely separated dorsally. *Raricirrus variabilis* differs from *R. beryli* in lacking the ciliated region anterior to the mouth opening and on the ventral surface of the first two setigers.

Epitokous individuals of *R. maculatus* have not been encountered while a single immature male epitoke of *R. beryli* has been described (Petersen & George 1991). The epitoke of *R. beryli* was smaller (11 mm) than the benthic form, with elongate capillary setae approximately 150% of the body width. The epitokous individuals of *R. variabilis* are (with one exception) much larger

(14–20 mm) than the benthic form with the elongate capillary setae only 75% of the body width.

Etymology. — The specific name refers to the variability in the distribution of setal types.

Discussion

The family Ctenodrilidae is now comprised of the subfamilies Ctenodrilinae and Raphidrilinae, each with two described genera. The genera *Ctenodrilus* Claparède, 1863, and *Aphropharynx* Wilfert, 1974, are united within the subfamily Ctenodrilinae by their lack of branchial filaments while the subfamily Raphidrilinae consists of the genera *Raphidrilus* Monticelli, 1910, and *Raricirrus* Hartman, 1961, both possessing branchiae. Morphological differences between *Raricirrus* and *Raphidrilus* are slight, however, and there has been some doubt as to whether their separation is justified (see discussion in Petersen & George 1991).

Based on the descriptions of *Raphidrilus nemasoma*, an analysis of the type material of *Raricirrus maculatus* and the analysis of specimens of *Raricirrus beryli*, Petersen & George (1991) retained separation of *Raphidrilus* and *Raricirrus* and identified several morphological characters that could be useful in differentiating these two genera. These characters include the position and extent of the heart body, the structure of the nuchal organs, the structure of the head region, and the presence of a region with modified setae.

Petersen & George (1991) had used the anteriormost occurrence of the heart body as a distinguishing character for the genera *Raphidrilus* and *Raricirrus*. That of *Raphidrilus nemasoma* has been reported to first appear at setiger 4 while that of the two previously known species of *Raricirrus* does not occur anterior to setiger 8 or 9 (Peterson & George 1991). Unfortunately this generalization does not hold true for *R. variabilis* as the heart body begins at setiger 4 (4–6) in the benthic specimens taken from the

wood panels and does not appear until setigers 8–10 in the epitokous individuals from the wild wood. The heart body of polychaetes has been viewed as being of hematopoietic function (Kennedy & Dales 1958) however, more recent work has indicated that this organ could also have a protective function. Vovelle et al. (1995) noted chemical differences in the heart bodies of specimens of *Raricirrus beryli* collected adjacent to and away from the North Sea oil platforms indicating a possible role in the detoxification of hydrocarbons in this polluted environment. While the anterior-most occurrence of the heart body seems to be a valid specific character and may possibly be related to the ability of a species to cope with its environment, it is not useful in the differentiation of genera.

Sokolov (1911) described the nuchal organs of *Raphidrilus* as often-closed slits with short cilia extending from the base of the pit while Petersen & George (1991) described those of *Raricirrus* as bare oval areas surrounded by fields of cilia. The majority of specimens of *R. variabilis* examined possessed slit-like nuchal organs with no visible ciliation of the surrounding prostomial surface when viewed using scanning electron microscopy. Several specimens that were observed under the dissecting microscope had the rims of their nuchal organs widely expanded, exposing what appeared to be a uniformly ciliated surface within. The morphology of the nuchal organs of *R. variabilis* is more similar to that described for the genus *Raphidrilus* than for *Raricirrus*. However, while the ultrastructure of nuchal organs has been utilized in the recognition of possible phylogenetic relationships among polychaete families (Purschke 1986), the use of their gross morphology as a taxonomic character at the generic level is questionable. Nuchal organs may be eversible (Whittle & Zahid 1974) with associated retractor muscles (Purschke 1986) and may vary in morphology at reproductive maturity, perhaps exhibiting sexual dimorphism

(Schlötzer-Schrehardt 1987, 1991). This variability in the morphology of nuchal organs within a species as well as a lack of knowledge regarding nuchal organ variability within a family or genus precludes their use (at the light microscope level) in differentiating between these two genera.

Petersen & George (1991) also referred to the shape and arrangement of the head as perhaps being of possible taxonomic significance. The prostomium, peristomium, and first setiger of *Raricirrus beryli* and *R. maculatus* are described by Petersen & George (1991) as forming a single “visual unit” with all these segments united along the dorsal surface. In the figures of Monticelli (1910) and Sokolov (1911) the prostomium and peristomium of *Raphidrilus nemasoma* appear to be united dorsally while the first setigerous segment is clearly separated from these segments. The prostomium, peristomium and first setigerous segment of *R. variabilis* are also united dorsally and this character may be of utility in the separation of *Raphidrilus* and *Raricirrus*. Further analysis of material belonging to the genus *Raphidrilus* would be required to substantiate the use of this morphological character in separation of the two genera.

Raricirrus variabilis is placed within the genus *Raricirrus*, rather than *Raphidrilus*, primarily due to its setal characteristics. *Raphidrilus nemasoma* is described as possessing only capillary notosetae and neurosetae with the exception of several modified segments possessing thick spines (Monticelli 1910, Sokolov 1911). *Raricirrus variabilis*, as well as the other two described species in this genus, possesses both serrate capillaries and coarsely serrate setae in their notopodia. *R. variabilis* differs from the other species in the possession of short, coarsely serrate falcate spines (Fig. 3A) in the anterior notopodia while *R. maculatus* and *R. beryli* both have long, natatory capillaries in their “dispersal” forms (Petersen & George 1991). The finely pectinate falcigers, grading to coarsely serrate forms posteri-

orly, are characteristic of all three species in the genus.

Based on the analysis of *Raricirrus variabilis*, the generic diagnosis for *Raricirrus* Hartman, 1961 emended by Petersen & George 1991, is further emended as follows: *Raricirrus* Hartman, 1961, emended.

Type species. — *Raricirrus maculatus* Hartman, 1961, by monotypy and original description.

Diagnosis. — Raphidrilinae with prostomium not obviously delimited from peristomium and setiger 1 dorsally; with or without ventral cilia on peristomium and first few segments; last 6–9 setigers shorter and wider than preceding ones, forming a distinct posterior region. Branchiae simple, filamentous, may be clublike distally. Heart body in variable number of anterior and middle segments. Notosetae serrate capillaries and coarsely serrate forms posteriorly, some species also with short pectinate fal-cigers; neurosetae falcate and finely pectinate anteriorly, grading to coarsely serrate forms posteriorly; simple curved spines sometimes replacing most or all normal setae in 1 or 2 modified posterior segments of some species. With or without seminal vesicle and reproductive stylet.

Remarks. — *Raricirrus variabilis* is an example of an opportunist in the deep sea which survives by finding and exploiting organically enriched sites (Grassle & Morse-Porteous 1987). The two previously described species in the genus are also reported from environments with elevated levels of organic carbon being most positively correlated with elevated levels of hydrocarbons. *Raricirrus maculatus* is known from an area close to an industrial waste discharge site in fine sediments that are contaminated with heavy metals and chlorinated hydrocarbons (Hartman 1961, Petersen & George 1991). *Raricirrus beryli* was first reported at low densities from a sewage sludge dumping ground and at very high densities in fine sediments with high hydrocarbon concentrations from northern North

Sea oilfields (Moore 1991, Petersen & George 1991). *Raricirrus beryli* has also been collected by A. Norrevang in shallow (5 m) waters in Skopun Harbor in the Faroes, a harbor without any apparent elevated hydrocarbon input (Petersen 1994 pers. comm.). Based on strong association with high concentrations of certain components of the aromatic fraction of hydrocarbons, Moore (1991) has characterized *R. beryli* as a polychaete indicator species for sediments containing pollution levels of hydrocarbons. The epitokes and/or larvae of *R. variabilis* are most likely attracted to sites in the deep sea with high concentrations of organic material such as decaying wood.

The largest eggs observed in female epitokes (Table 1, specimen U) of *Raricirrus variabilis* were approximately 140 μm in diameter. While any determination of mode of development based on egg size should be done with great caution (Bridges 1993), it is probable that this species has either direct development or a short lecithotrophic larval mode of development. Assuming that these eggs approximate egg size at maturity, their diameter compares favorably with those of the unknown species of *Raphidrilus* (*Raphidrilus nemasoma* (sic)) studied by Qian & Chia (1989). By following the development of newly fertilized eggs, Qian & Chia found that the eggs of *Raphidrilus* sp. developed directly into free-crawling preadults. Similarly the eggs of *R. variabilis* may produce preadults through direct development subsequent to deep-sea dispersal by the epitokous body form. Bridges (1993), for example, has reported a lecithotrophic mode of development for a morph of *Streblospio benedicti* with eggs 100–200 μm in diameter and it is also quite possible, based upon egg diameter, that *R. variabilis* may also have a lecithotrophic mode of development rather than direct development. Additionally, dispersal may also be accomplished by some type of asexual dispersal form similar to that reported for *R. beryli* by Petersen & George (1991).

Two body forms were recognized in *Raricirrus variabilis*, a "normal" benthic form and a form similar to what Petersen & George (1991) identified as an epitokous phase for *R. beryli*. They considered this body form as an epitoke because it was sexually mature with the body usually packed with gametes. The epitokous form of *R. variabilis* was loosely organized with much free movement of the numerous large eggs within the interior of the worms. This may have been an artifact of poor fixation or may be indicative of the transient nature of this life stage with the individuals reduced to little more than egg containers. The epitoke of *R. variabilis* differs from the one immature male epitoke of *R. beryli* described by Petersen & George (1991) in that its capillaries are only 0.75 times the body width while those of *R. beryli* were about 1.5 times body width.

Petersen & George (1991) also described a third body form they referred to as a "dispersal" form which had capillaries 2–4 times the body width but with no obvious gametes. Petersen & George (1991) hypothesized that this dispersal form may disperse, settle and then develop into spawning epitokes. There were no specimens of *R. variabilis* recovered, from the wood panels or the piece of wild wood, that were analogous to the dispersal phase recognized for *R. beryli*.

Many specimens of the two shallow-water species, *R. beryli* and *R. maculata*, examined by Petersen & George (1991) displayed evidence of regeneration subsequent to fragmentation. Both of these species seem to rely on asexual reproduction as a means of exploiting their high organic, high hydrocarbon content, environment. Following colonization of a patch of suitable habitat by some type of dispersal form, asexual reproduction would provide a means of rapid population growth in order to better utilize the available resource (Schroeder & Hermans 1975).

There was no evidence of an asexual re-

productive stage for *R. variabilis* (although the possibility exists that temporally restrictive sampling could have missed such an asexual stage if it were a seasonal event). This species seems to have adapted a different reproductive strategy in the exploitation of its patchily distributed resource. Many specimens of the benthic form of *R. variabilis* contained both developing eggs and sperm and were evidently hermaphroditic. Hermaphroditism has often been associated with patchy, unpredictable environments (Petraitis 1991) and may allow *R. variabilis* to enhance its exploitation of widely scattered patches of organic material on the deep-sea floor. The benthic form could function as both genders or as the gender which would maximize reproductive success under existing environmental conditions similar to the strategy proposed for *Capitella capitata* by Petraitis (1991).

Once established on a patch of suitable organic resource, the benthic form of *R. variabilis* may engage in sexual reproduction, maximizing its reproductive success through its hermaphroditism. The resultant free-living larvae would increase the population size at the home site although at a reduced rate when compared to the exploitation of a comparable resource in shallower waters. Some of the benthic individuals could develop into the epitokous form, either as a routine percentage of the population as seen in *Dedocaceria caulleryi* Oersted (Gibson & Clark 1976) or perhaps in response to deteriorating resource, as a means of colonizing suitable habitat elsewhere.

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